

Population structure, diet, and bioenergetics of introduced Smallmouth Bass in an Intermountain West reservoir

SKYLAR L. WOLF^{1,*}, NATALIE BOREN², BENJAMIN VASQUEZ^{2,3}, JACK DUDDING¹, AND ROBERT SHIELDS¹

¹Utah Division of Wildlife Resources, Fisheries Experiment Station, 1465 W. 200 N., Logan, UT 84321

²Utah Division of Wildlife Resources, Northeast Region Office, 318 N. Vernal Ave., Vernal, UT 84078

³Present address: Wisconsin Cooperative Fishery Research Unit, College of Natural Resources, University of Wisconsin–Stevens Point, 800 Reserve Street, Stevens Point, WI 54481

ABSTRACT.—Smallmouth Bass *Micropterus dolomieu* is a recreationally important sport fish throughout much of North America, but population metrics are lacking in the Intermountain West, where the species is not native and where its performance may differ from other geographic portions of its range. We characterized population structure and condition, growth, and the feeding habitats and bioenergetics of a self-sustaining Smallmouth Bass population in Starvation Reservoir, located in northeast Utah. In this reservoir, Smallmouth Bass may experience environmental conditions (e.g., shorter growing season and greater water-level fluctuation) that are uncommon to other portions of its range. We found growth rates to be intermediate within the context of surveyed populations across its distribution, with fish reaching quality length (280 mm TL) at approximately age 4 and relative growth index values ranging from 86 to 112 for fish ages 2–10. Fish condition (relative weight) was at or above average across all size classifications encountered (stock, quality, preferred, and memorable), and diet analyses indicated that fish used a variety of prey types that differed by season. Bioenergetics models indicated that proportional feeding was highest for age-2 fish ($P = 0.54$) and declined incrementally through age class, relating to trends of relative growth. Our results suggest that the Smallmouth Bass population in Starvation Reservoir is performing well within the constraints of a midelevation, Intermountain West reservoir. Our study may provide managers with useful data to compare with other Smallmouth Bass populations in this geographic region.

RESUMEN.—La lubina de boca chica *Micropterus dolomieu* es un pez deportivo de importancia recreativa en gran parte de América del Norte, pero se carece de métricas poblacionales en el oeste intermontañoso, donde la especie no es nativa y su desempeño puede diferir de otras partes geográficas de su área de distribución. Caracterizamos la estructura, la condición, el crecimiento, los hábitats de alimentación y la bioenergética de una población autosuficiente de lubina de boca chica en el embalse de Starvation, situado en el noreste de Utah. En este embalse, la lubina de boca chica puede experimentar condiciones ambientales que son poco comunes en otras partes de su área de distribución (e.g. una temporada de crecimiento más corta y una mayor fluctuación del nivel del agua). Las tasas de crecimiento fueron intermedias en el contexto de las poblaciones estudiadas a lo largo de su distribución, con peces que alcanzaron una longitud de calidad (280 mm TL) aproximadamente a la edad de cuatro años y valores de índice de crecimiento relativo que oscilaron entre 86 y 112 en las edades de dos a 10. La condición de los peces (peso relativo) fue igual o superior al promedio en todas las clasificaciones de tamaño encontradas (stock, calidad, preferido y memorable), y los análisis de la dieta indicaron que los peces utilizaban una variedad de tipos de presas que diferían según la estación. Los modelos bioenergéticos indicaron que la alimentación proporcional fue más alta para los peces de dos años ($P = 0.54$) y disminuyó gradualmente a través de las clases de edad, en relación con las tendencias de crecimiento relativo. Nuestros resultados sugieren que la población de lubina de boca chica en el embalse de Starvation es exitosa dentro de las limitaciones de un embalse de altitud media en el oeste de las montañas. Nuestro estudio puede proporcionar una comparación útil para los gestores de otras poblaciones de lubina de boca chica en esta región geográfica.

Smallmouth Bass *Micropterus dolomieu* is a popular sport fish with a broad distribution, requiring biologists to manage the species across a gradient of environmental conditions that may affect its population performance. The native range of Smallmouth Bass encompasses

much of central and eastern North America (Scott and Crossman 1998), where it performs well in both lentic and lotic environments (Brewer and Orth 2015). Additionally, its distribution has expanded beyond its native boundaries into portions of the eastern Atlantic

*Corresponding author: Skylar.L.Wolf@gmail.com

SLW  orcid.org/0000-0001-7469-3012

slope drainage (MacCrimmon and Robbins 1975) and the western United States (Carey et al. 2011) as a result of anthropogenic transport (e.g., stocking). These stocking events increase angling opportunities and have subsequent economic benefits for the region (Carey et al. 2011, Seguy and Long 2021). The recreational and economic importance of Smallmouth Bass has driven natural resource management agencies to actively manage this species (see Paukert et al. 2007 for an overview) including various creel limits (Buynak and Mitchell 2002), length regulations (Newman and Hoff 2000), and seasonal restrictions (Quinn 2002). Foundational to guiding these management actions are data on the population structure and performance of Smallmouth Bass, requiring information on growth and mortality that is often region specific and dictated by environmental characteristics like temperature and food availability.

Growth (e.g., mean length-at age) and mortality (e.g., total annual mortality) standards are useful for managers to make comparisons and evaluate the performance of specific sport fish populations. Growth standards exist for Smallmouth Bass (e.g., Jackson et al. 2008); however, condition-specific variability in growth (e.g., lentic vs. lotic systems—Schall et al. 2016, Starks and Rodger 2020; latitude and elevation—Beamesderfer and North 1995) suggests the need for additional considerations when comparing spatially or temporally separated populations. Because both coarse-scale (e.g., climate—Dunlop and Shuter 2006) and fine-scale factors (e.g., habitat—Whitledge et al. 2006) influence growth rates of Smallmouth Bass, growth comparisons may be best applied within the scope of similar systems. For example, the growing season that Smallmouth Bass experience varies along a latitudinal gradient (Mullner and Hubert 1993, Beamesderfer and North 1995, Patton and Hubert 1996). Similarly, mortality may vary between populations, resulting from differing environmental conditions (Beamesderfer and North 1995), exploitation rates (Paragamian 1984), and management-driven decisions such as protective harvest regulations to improve size structure (Newman and Hoff 2000). Smallmouth Bass annual mortality may reach 0.50 in some populations (Paragamian 1984, Austen and Orth 1988, Hoff 1995) as a combined result of fishing and natural mortality but can be highly variable

within the same state or region. For example, annual mortality ranged from 0.22 to 0.61 in Nebraska Reservoirs (Schall et al. 2016). High variability in mortality suggests that additional factors such as prey availability could contribute to observed trends.

Prey availability can affect both growth and mortality of fishes (Hoxmeier et al. 2004); thus, both diet analysis and bioenergetics modeling may provide valuable insight to the performance of a fishery. Smallmouth Bass are considered apex predators in smaller stream systems (Roell and Orth 1993), whereas in larger rivers or lentic environments (e.g., lakes and reservoirs), they may interact with other predatory fishes (e.g., native salmonids—Zanden et al. 2004; Walleye *Sander vitreus*—Wuellner et al. 2010) over common resources. Common forage items used by Smallmouth Bass throughout North America include crayfish (Probst et al. 1984, Roell and Orth 1993, Luecke et al. 2001), various fishes (Dauwalter and Fisher 2008, Wuellner et al. 2010), and, to a lesser extent, other aquatic invertebrates (i.e., in addition to crayfish—Olsen and Young 2003, Wuellner et al. 2010). Diet composition often reflects prey availability (Beck 2013); however, additional factors like size selectivity (Stein 1977, Gaeta et al. 2018) and environmental conditions (e.g., turbidity—Carter et al. 2010) may contribute to observed consumption patterns. Consumption rates of fishes are often characterized using bioenergetics models, which incorporate prey energy density and thermal experience into dietary analyses and allow managers to determine consumption as a function of realized growth and diet. Bioenergetics are useful for inference on prey availability and can provide insight on limitations to growth and overwinter survival when combined with information on fish growth and condition (Lyons 1997).

The importance of Smallmouth Bass as a sport fish is reflected in an extensive body of peer-reviewed work addressing the species' population characteristics. Unfortunately, the Intermountain West region is underrepresented in these evaluations due to the relatively recent addition of this species to reservoirs and flowing waters (see Fuller et al. 2021). Environmental factors including elevation, latitude, and habitat, coupled with water-level fluctuation and flooding, affect stream and reservoir productivity in this region

(Beamesderfer and North 1995). Combined, these environmental characteristics dictate both temperature regimes (Mullner and Hubert 1993) and feeding habits (Fullerton et al. 2000) and may influence the growth potential and annual mortality of Intermountain West Smallmouth Bass populations in ways that are uncommon to its native range. Baseline data on Smallmouth Bass populations in the Intermountain West are lacking, and studies assessing population metrics (e.g., growth, mortality, and feeding habits) in this region would provide useful comparisons for other populations in the region.

Starvation Reservoir supports several recreational species, including Smallmouth Bass, and is a popular fishing destination for anglers located in the Intermountain West. The species composition and subsequent management of Starvation Reservoir have changed considerably over the course of the reservoir's history. Upon dam completion in the early 1970s, Starvation Reservoir was initially managed as a successful Rainbow Trout *Oncorhynchus mykiss* fishery. During this period, Utah Chub *Gila atraria* abundance increased greatly in response to drought and low reservoir levels that favored Utah Chub survival over stocked trout. In response to increases of Utah Chub, Largemouth Bass *Micropterus salmoides*, Smallmouth Bass, and Walleye were stocked from 1977 through 1984 in an attempt to create a sport fishery that could use the Utah Chub as forage in littoral areas of the reservoir. Smallmouth Bass have persisted without supplemental stocking; however, abundance and recruitment of the population have been variable. For example, electrofishing surveys conducted by the UDWR in 1986 indicated that Smallmouth Bass was the most abundant species captured in the reservoir, whereas electrofishing surveys from 1992 through 1995 showed dramatic declines in Smallmouth Bass abundance relative to other species (Crosby and Johnson 1995). Additionally, diet analyses were performed in 1996–1998 (Ryals et al. 1999, Luecke et al. 2001), though the scope of this work was limited to diet composition without relation to fish condition or bioenergetics. Currently, Smallmouth Bass constitute an important recreational fishery in Starvation Reservoir. The fishery is managed with a 6-fish creel limit and no length regulation; however, harvest

estimates suggest that the fishery is primarily catch and release (Birchell et al. 2016).

Despite the recreational importance of Starvation Reservoir, detailed evaluations of the Smallmouth Bass population have been lacking; our study constitutes the first formal evaluation of Smallmouth Bass growth, mortality, and feeding in over 20 years. Consequently, the goal of our study was to characterize the current state and performance of Smallmouth Bass in Starvation Reservoir, in turn providing a useful comparison with other populations in the Intermountain West. To address this goal, we pursued the following objectives: (1) define the size structure and condition of the Smallmouth Bass population, (2) assess growth rates, mean length-at-age, and annual mortality, and (3) characterize diet and feeding efficiency using bioenergetics modeling across the growing season. The results of our study not only provide insight into the current state of a popular Smallmouth Bass fishery, but they also allow managers to take steps to improve this fishery as needed (e.g., increase forage base, promote harvest, etc.). More broadly, our findings provide managers with population information specific to the Intermountain West and can provide a useful comparison for future evaluations in similar reservoir ecosystems.

METHODS

Study Area

We conducted our study in Starvation Reservoir; a 14.1-km² (3495-surface-acre) mesotrophic reservoir (Crawford 2020) located near Duchesne, Utah (Fig. 1). Starvation Reservoir straddles the Uinta Basin floor and the Semi-arid Benchlands and Canyonlands (level IV ecoregions). The climate at the reservoir is semiarid, with little rainfall and variable seasonal temperatures (average minimum and maximum air temperatures: -18°C and 0°C , respectively, in January; 10°C and 33°C , respectively, in July—Woods et al. 2001). The reservoir is an impoundment of the Strawberry River completed by the Bureau of Reclamation in 1972 as part of the Central Utah Project. It is located at an elevation of 1700 m (5700 ft) and at full pool has average and maximum depths of 19.8 m (65 ft) and 42.2 m (155 ft), respectively. Most habitat in the reservoir is pelagic with steep breaks

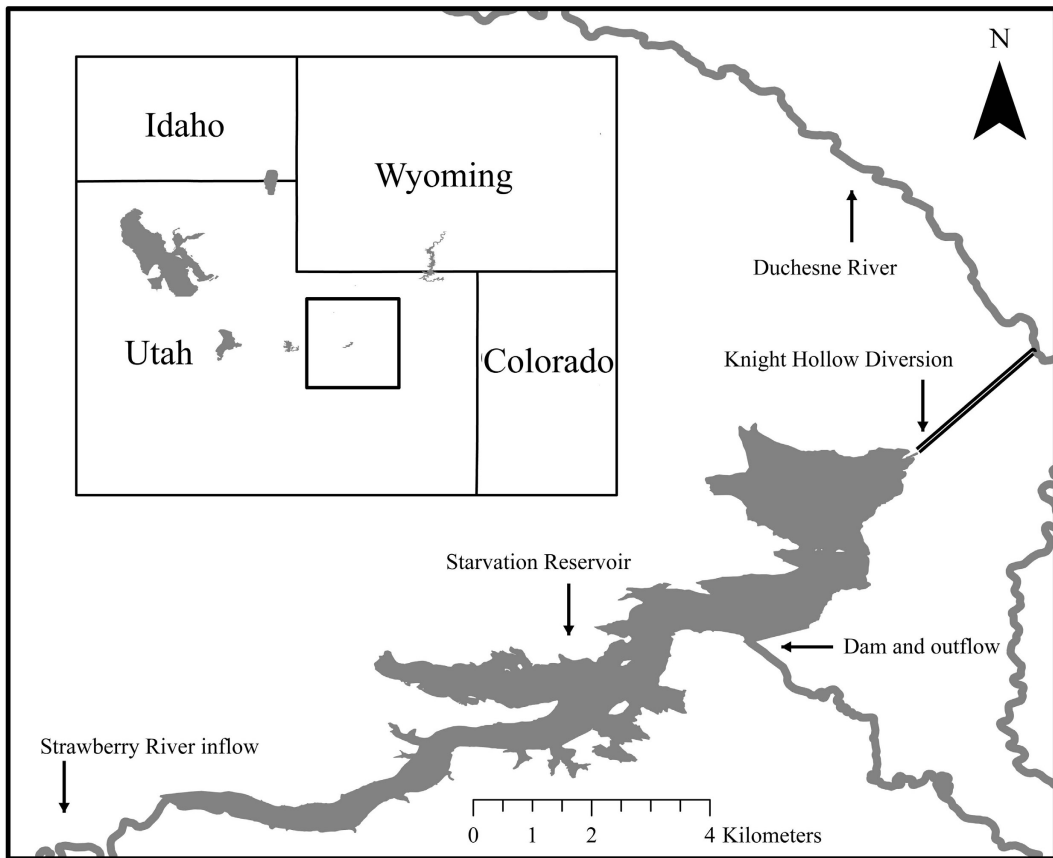


Fig. 1. Overview of Starvation Reservoir, located approximately 5 km northwest of Duchesne, Utah. The reservoir is filled by the Strawberry River (west) and the Knight Hollow Diversion (east), a diversion of the Duchesne River. Map insert indicates the location of Starvation Reservoir (box) within Utah. Additional reservoirs are Bear Lake (UT and ID), Flaming Gorge (WY and UT), and the Great Salt Lake, Utah Lake, and Strawberry Reservoir (UT; left to right).

outlining the flooded canyon. Submerged habitat consists mainly of rocky shoreline and sandy substrate, with some flooded vegetation (e.g., grasses) occurring during higher water levels in the spring. Water in Starvation Reservoir is primarily managed for local irrigation, causing large drawdowns in the volume of water present throughout the summer and fall (Central Utah Water Conservancy District 2021).

Field Collections

We deployed temperature loggers and sampled Smallmouth Bass from June through October 2020. We set temperature loggers (Hobo Pendant, Onset, Bourne, MA) at 2 locations and 3 depths (~3 m, 13 m, and 25 m) to provide thermal data for this study (bioenergetics model). Multiple depths provided

flexibility in assigning temperature for bioenergetics modeling and allowed us to identify the approximate period that lake turnover (i.e., mixing) occurred. When needed, additional water temperature data were derived from linear regression models using air temperature (see bioenergetics methods). Monthly air temperature averages during our study were comparable (± 3 °C) to averages recorded in the previous 5 years (NOAA station USC00422253, Duchesne, UT; NOAA 2022), and we assumed that water conditions during our study were representative of the reservoir during an average year under current conditions.

We sampled Smallmouth Bass throughout the reservoir using several gears during 17–27 June (electrofishing and angling), 22–24 July (electrofishing), and 14–19 October (gill nets) in 2020. Angling (by a combination of tournament

competitors and UDWR biologists) was used to supplement the collection of ageing structures in June. Fall netting (AFS standard benthic gill net, see table A.3 in Bonar et al. [2009] for specifications) provided diet samples for Smallmouth Bass in October once the fish had moved into deeper habitat. For other components of our study that required sample structure to be proportional to the underlying size structure of the population (e.g., weighting of the growth model and catch-curve analysis, discussed below), we used fish collected from spring nighttime electrofishing (Bacula et al. 2011). Electrofishing was conducted using direct current at a frequency of 60 Hz and a duty cycle of 25. Peak current (amps) ranged from 18 to 21 and was adjusted based on water conductivity using standardized electrofishing guidelines (Miranda 2009). All captured Smallmouth Bass were weighed (g) and measured for total length (mm). In addition, we collected ageing structures to facilitate growth estimation. All fish were released alive, and we did not attempt to collect sex information for growth analysis because we made comparisons to generalized indices (e.g., relative growth index, see analysis section). All ageing structures were collected in June from fish sampled using electrofishing or angling. We used a subsampling design for structure collection in which we targeted 10–20 individuals per 20-mm length bin. We chose dorsal spines because of high precision (Morehouse et al. 2013) and because their accuracy has been corroborated with otoliths in other northern populations (Walrath et al. 2015). We collected the second anterior dorsal spine by clipping it as close to the dorsal surface as possible (Isermann et al. 2003). Spines were individually placed in labeled coin envelopes and allowed to air dry. We collected stomach contents from Smallmouth Bass across the approximate growing season in Starvation Reservoir to characterize seasonal diet habits and provide inputs for bioenergetics modeling. Diet collections occurred in June, July, and October 2020 using gastric lavage as outlined by Hyslop (1980). Flushed stomach contents from each individual were placed in bags filled with 95% ethanol for storage and laboratory analysis.

Sample Processing

After drying, we mounted each dorsal spine in separate 1.5-mL labeled centrifuge tubes

using clear resin (Polytranspar Artificial Water, Granite Quarry, NC) following the methods of Koch and Quist (2007). We sectioned each spine (~1 mm) close to its base using a low-speed saw (Buehler IsoMet, Lake Bluff, IL). Sections were lightly sanded using progressively finer sandpaper (320, 600, and 2000 grit) and mounted to a microscope slide for viewing. Each slide was viewed independently by 3 readers without knowledge of the length or weight of the fish, and an age was assigned by counting the number of annuli present. Because fish were collected in June at the beginning of the growing season (Mullner and Hubert 1993), the final annulus occurred on the outer edge of each sectioned spine and represented the most-recent winter (i.e., period of slow growth). Age assignments among the 3 readers were compared, and a consensus age was assigned if at least 2 of 3 readers agreed on an age and the third reader differed by only ± 1 . In instances where these criteria were not met, we re-read the structure in concert and discussed the observations to reach a consensus.

Preserved stomach contents were drained with a fine-mesh cloth to remove ethanol and then weighed by prey category: (1) crayfish, (2) aquatic invertebrates (i.e., other than crayfish), (3) terrestrial insects, (4) zooplankton, and (5) fish. The number of crayfish and fish in each stomach were counted when possible, but other prey items were not counted due to their high prevalence and fragmentation in diet samples. We identified prey fishes to the species level; when prey fish were too digested to be identified, we used a key based on cleithra (Traynor et al. 2010) to determine the lowest taxonomic ranking. Aquatic invertebrates found in a subset of Smallmouth Bass diets collected in June and July were identified to the order level to provide further information on feeding patterns. Items excluded in analysis were non-prey items (e.g., soft plastics, wood, vegetation, rocks) and prey determined to be angler bait (earthworms during tournament angling), which occurred in 1.1% of processed diets.

Statistical Analysis

We used length and weight data to construct length–weight regression models and to summarize population structure and condition in terms of proportional size distribution

(PSD; formerly proportional stock density—Guy et al. 2007) and relative weight (W_r —Murphy et al. 1991). We constructed separate length–weight regression models for June and October to account for changes in weight as a function of both length and increased feeding throughout the growing season. Similarly, we calculated W_r from samples collected in both June and October to account for potential seasonal differences (Bacula et al. 2011). Relative weight was calculated by dividing the recorded weight of each fish by its corresponding standard weight (Kolander et al. 1993) and multiplying by 100. Calculations of PSD were derived from length criteria presented in Gabelhouse (1984). We summarized W_r by PSD length category (stock, quality, preferred, memorable, and trophy; Table 3).

We used our length-at-age data to construct a von Bertalanffy growth model (VBGM) using a weighted adjustment to account for the effect of subsampling across length bins (Bettoli and Miranda 2001, Goodyear 2019). To fit the VBGM, we used a weighted aged-only sample following recommendations of Hilling et al. (2020) and Lusk et al. (2021). We weighted our aged data set using the size structure of the population (determined by spring electrofishing). To weight each length bin, we used the equation provided in Chih (2009):

$$RW_i = \frac{NL_i / TN}{OL_i / TO},$$

where RW is the reweighting factor belonging to length interval i , NL is the number of fish belonging to length i encountered in the field, TN is the total number fish encountered in the field, OL is the number of ageing structures collected in length interval i , and TO is the total number of ageing structures in the sample.

To build our growth model, we used the FSA package (Ogle et al. 2021) in program R (Version 3.6.3—R Core Team 2020). The VBGM was used to produce parameter estimates of t_0 (model intercept), k (Brody growth rate coefficient), and L_∞ (average maximum length of a fish in the population; von Bertalanffy 1938). We bootstrapped the model parameters ($N = 2000$ iterations) using the R package ‘*nlstools*’ (Florent et al. 2015) to achieve stabilized (i.e., consistent) mean estimates and

a more robust standard error. Lastly, we generated mean length-at-age estimates, which we used to calculate the relative growth index (RGI; Quist et al. 2003) following the Smallmouth Bass equation presented in Jackson et al. (2008).

We used catch-curve data to estimate instantaneous (Z) and annual (A) mortality. First, we used our aged subsample to construct an age–length key using methods described in Isermann and Knight (2005) and the FSA package (Ogle et al. 2021). We assigned ages to un-aged fish using our age–length key. We estimated Z using the Chapman–Robson method (Chapman and Robson 1960). The Chapman–Robson method has performed well in several evaluations (Dunn et al. 2002) and was better suited for our smaller sample size (Smith et al. 2012) that fell below the recommendations for catch-curve regression ($n = 500$ – 1000 ; Coggins et al. 2013). We truncated our data using the “peak plus criterion” (first age group used being one year older than the age of peak abundance) following the recommendations of Smith et al. (2012).

We enumerated stomach contents by frequency of occurrence (Macdonald and Green 1983) and wet weight as a proportion of an individual’s consumption. Frequency of occurrence for each prey item was calculated as a presence-absence statistic in each stomach, and the resulting metric represented the proportion of total stomachs that contained that prey type. Proportional wet weight was determined using the total mass of a prey category identified in an individual stomach divided by the total mass of the stomach sample. We used both measurements as a way to determine importance of diet items.

We developed bioenergetics models for Smallmouth Bass in Starvation Reservoir to estimate the amount of prey consumed, feeding rates as a proportion of maximum consumption (p), and growth efficiency (GE). We modeled prey consumption for age 2–9 Smallmouth Bass separately because growth (i.e., annual increase in weight) differs with age. We truncated our data to age 9 because few Smallmouth Bass lived beyond this age in Starvation Reservoir (i.e., growth data were limited). We used the same diet proportions for each age class because Smallmouth Bass undergo an ontogenetic shift in diet at a

TABLE 1. Mean length-at-age, growth, start and end weights (g), and bioenergetics model results for Smallmouth Bass in Starvation Reservoir. Mean length (total length, mm) was estimated using our weighted growth model fit to length-at-age data. Relative growth index (RGI) values were calculated using the equation presented in Jackson et al. (2008). Mean weight for June was estimated for the corresponding age using a June-specific length-weight regression equation, and it served as the starting weight for each bioenergetics model. Mean weight for October was estimated using the length of the next age class and an October-specific length-weight regression, and it served as the ending weight for each bioenergetics model. For length and weight columns, 95% confidence intervals (95% CI) are presented. Bioenergetics model results for each age class are presented in terms of feeding as a proportion of maximum consumption (p), amount consumed (Cons.) on a per-fish basis, and the growth efficiency (GE) in terms of observed growth (June to October weight change) divided by prey consumed.

| Age | Mean length (95% CI) | RGI | June weight (95% CI) | October weight (95% CI) | p | Cons. (g) | GE |
|-----|----------------------|-----|----------------------|-------------------------|------|-----------|------|
| 2 | 193 (176–211) | 112 | 96 (94–98) | 190 (188–192) | 0.54 | 571 | 0.16 |
| 3 | 237 (227–247) | 99 | 178 (176–180) | 296 (294–298) | 0.43 | 673 | 0.18 |
| 4 | 273 (264–282) | 93 | 272 (270–274) | 406 (404–408) | 0.37 | 748 | 0.18 |
| 5 | 302 (293–311) | 90 | 370 (368–372) | 516 (514–518) | 0.33 | 806 | 0.18 |
| 6 | 326 (315–335) | 89 | 466 (464–468) | 616 (614–618) | 0.30 | 842 | 0.18 |
| 7 | 345 (331–335) | 87 | 553 (551–555) | 710 (710–712) | 0.28 | 878 | 0.18 |
| 8 | 361 (341–379) | 87 | 634 (632–636) | 793 (791–795) | 0.25 | 900 | 0.18 |
| 9 | 374 (384–398) | 86 | 705 (703–707) | 869 (867–871) | 0.25 | 924 | 0.18 |
| 10 | 385 (354–416) | 86 | 770 (768–772) | NA | NA | NA | NA |

length below our age-2 fish (~125 mm TL; Olson and Young 2003, Dauwalter and Fisher 2008). We ran our bioenergetics models over a 150-day period (approximately 1 June through 31 October) to encompass the approximate time frame during which feeding and growth occurred. We assumed feeding to be limited and have a negligible effect on growth outside of this time frame because of low water temperatures (Webster 1954, Coutant 1975). For each age class, we assigned a starting and ending weight based on length-at-age predictions and our length-weight regressions developed from fish captured in June and October (Table 1). Consumption (grams of prey) was estimated for the entire 150-d period. We estimated p as the proportion of observed consumption compared to a temperature and size-specific maximum consumption rate (as determined by the model). Lastly, we estimated GE by dividing the weight change in fish (growth in grams over 150 d) by the estimated prey consumed over the same period. Both p and GE are useful descriptors of growth performance, with p informing on the quantity of prey available and GE informing on the quality of prey available (Koehler et al. 2006).

We fit our bioenergetics models using Fish Bioenergetics 4.0 (Deslauriers et al. 2017) in program R. Within Fish Bioenergetics 4.0, we used the Smallmouth Bass model developed by Whitley et al. (2003), which is specific to growth at temperatures ≤ 26 °C. We specified model inputs for prey proportion (mass by wet weight), prey and predator energy density (J/g) and thermal experience (temperature, °C). Prey proportions were assigned using data from June samples for the first 30 days, data from July samples for days 31–90, and October samples for days 91–150. For prey energy density, we reviewed literature and assigned values relevant to our study and prey species (Table 2). For thermal experience, we used the daily average of hourly temperature readings recorded at the uppermost temperature loggers in Starvation Reservoir (~3 m from surface; Fig. 2). In instances where data gaps occurred (e.g., missing temperature loggers), we used a linear regression model ($R^2 = 0.95$) to predict water temperatures that we developed using collected water temperature data and the 2-week moving average of minimum air

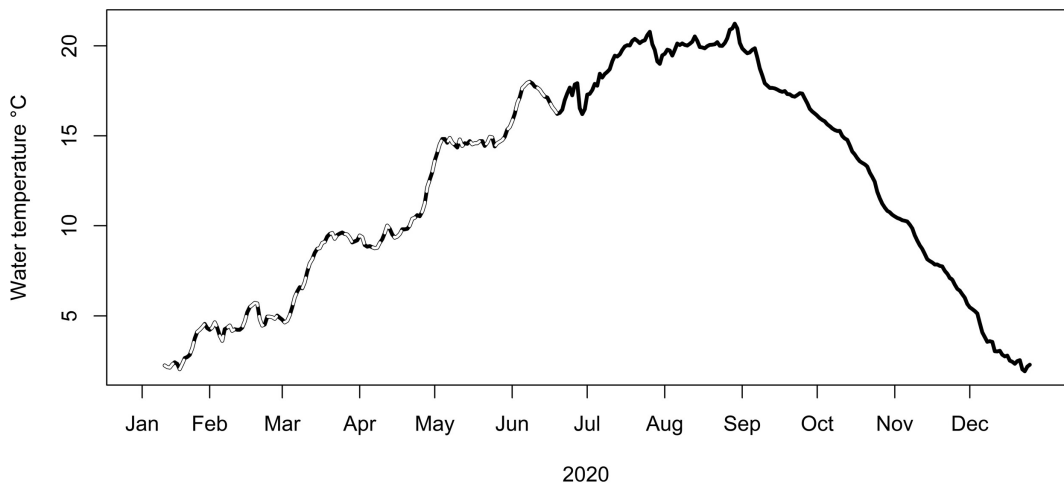


Fig. 2. Water temperature (~ 3 m below surface) in Starvation Reservoir during 2020. Data were collected using Hobo temperature loggers during June 2020. Additional temperature data were collected through April 2021 (data beyond December 2020 were not plotted). Using these water temperature data (June 2020–April 2021, solid line), a regression model was built using the 2-week moving average of minimum air temperatures to predicted water temperature for January–May 2020 (dashed line).

TABLE 2. Energy density by prey type used in bioenergetics modeling. All data are presented in terms of Joules per gram (J/g) wet weight. Values with multiple sources have been averaged between studies.

| Prey | Energy (J/g) | Source |
|-----------------------|--------------|--|
| Crayfish | 3500 | Cummins and Wuycheck 1971, Roell and Orth 1993, Yako et al. 2000 |
| Aquatic invertebrates | 3000 | Cummins and Wuycheck 1971, McCarthy et al. 2009 |
| Terrestrial insects | 5134 | McCarthy et al. 2009 |
| Fish | 4186 | Eggleton and Schramm 2002 |

temperatures from the nearest National Oceanic and Atmospheric Administration weather station (NOAA station USC00422253, Duchesne, UT; NOAA 2022). Temperature is an important resource to fishes (Magnuson et al. 1979); we chose to use thermal data from the upper depth strata for our model because we assumed that Smallmouth Bass would select thermal conditions closest to their optimum for growth (22 °C, Whitley et al. 2002). Our June and July sampling supported the idea that Smallmouth Bass inhabited and fed in shallow portions of the reservoir (e.g., around rocky banks). October netting suggested that some Smallmouth Bass moved to deeper habitats during fall; however, water temperatures were consistent across depth by this point (i.e., fall mixing was occurring), and continued use of temperature data collected in the upper depth strata was representative of the entire reservoir through the end of our modeled time period.

RESULTS

In total, we sampled 539 Smallmouth Bass from June through October 2020. We collected 407 Smallmouth Bass in June (257 electrofishing, 150 angling), 68 in July (electrofishing), and 64 in October (gill nets). We collected dorsal spines and aged 139 individuals sampled in June. Diet samples were collected from 175 individuals during June ($n = 99$), July ($n = 53$), and October ($n = 23$).

We found strong relationships between length and weight; metrics of PSD and W_r indicated a well-balanced population in good condition. We developed separate length–weight regression models for the beginning and end of the growing season. The resulting model equations were the following

$$\text{June, } \log_{(\text{weight})} = -4.92638 + 3.02181 \times \log_{(\text{length})}$$

and

$$\text{October, } \log_{(\text{weight})} = -5.16803 + 3.13561 \times \log_{(\text{length})},$$

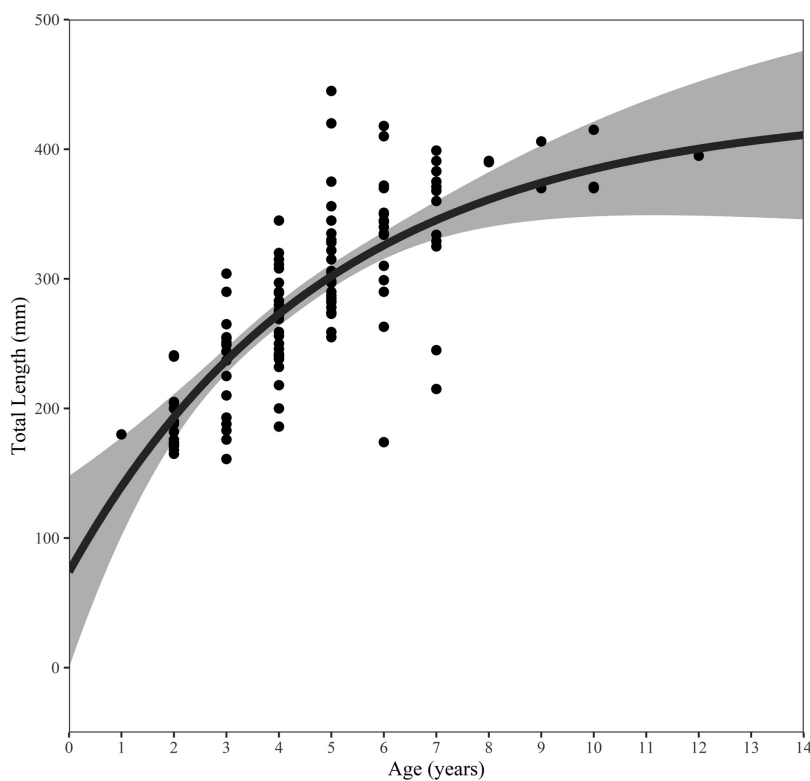


Fig. 3. Von Bertalanffy growth model for Smallmouth Bass collected in Starvation Reservoir, Utah, during the summer of 2020. Mean length-at-age is predicted (black line) with 95% confidence intervals around predictions shown (gray shading). Length-at-age data ($N = 139$) are plotted (black dots).

TABLE 3. Size structure and condition (with standard error in parentheses) of Smallmouth Bass collected in Starvation Reservoir, Utah. Size thresholds for each length category were derived from Gabelhouse (1984).

| Length category | Size threshold | PSD- X | Spring W_r | Fall W_r |
|-------------------|----------------|----------|------------------|------------|
| Stock | ≥ 180 mm | NA | 101 (3.8) | 100 (2.9) |
| Quality (PSD) | ≥ 280 mm | 49 | 102 (2.7) | 96 (2.0) |
| Preferred (PSD-P) | ≥ 350 mm | 14 | 92 (2.3) | 102 (1.6) |
| Memorable (PSD-M) | ≥ 430 mm | 2 | 111 ^a | 100 (2.8) |
| Trophy (PSD-T) | ≥ 510 mm | 0 | NA | NA |

^aSingle fish

where “weight” is the predicted weight (g) of a fish based on its total “length” (mm). Model fit was good for each model ($R^2 = 0.97$ for June, $R^2 = 0.98$ for October), and residual points were evenly distributed. As expected, PSD- X values declined exponentially with length category (Table 3). Condition of fish (W_r) fell within a range of 92 to 111 among length categories and season (Table 3).

We aged 139 dorsal spines and determined growth parameters for Smallmouth Bass in Starvation Reservoir (Fig. 3). Bootstrapped

VBGM parameter estimates and associated 95% confidence intervals were 434 (364–612) for L_∞ , 0.20 (0.08–0.36) for k , and -1.04 (-2.76 to 0.11) for t_0 . As expected, mean length-at-age estimates increased with age (Table 1). The maximum age recorded was 12. A residual plot of our VBGM indicated randomly distributed residuals, and we assumed adequate model fit. We found that RGI declined through each cohort. Age-2 fish had an RGI of 112, whereas the RGI of age-10 fish declined to 86. Using catch-curve data and

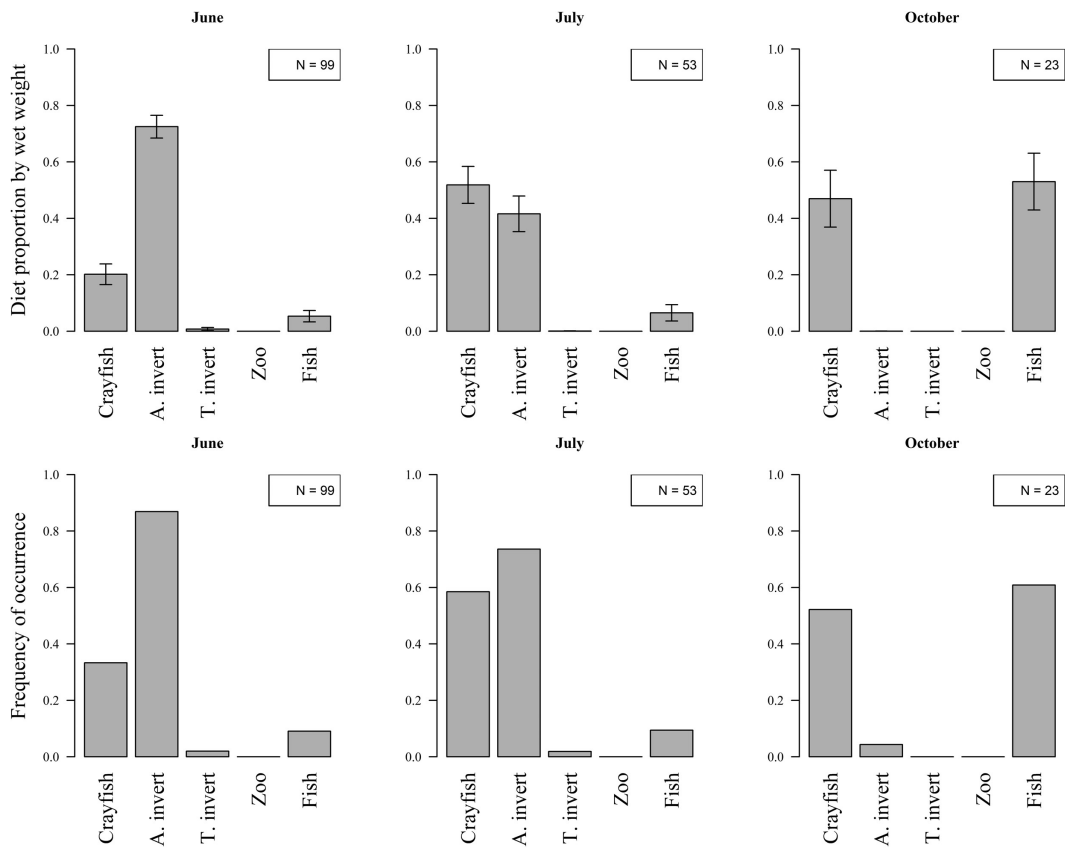


Fig. 4. Diet composition of Smallmouth Bass in Starvation Reservoir, Utah, during 2020. Diet proportion by wet weight represents the mean proportion of each diet item across all stomach samples by month, with standard error bars. Frequency of occurrence represents the number of stomachs containing each diet item, divided by the total number of stomachs collected during that month. A. invert = aquatic invertebrates, T. invert = terrestrial invertebrates, and Zoo = zooplankton.

the Chapman–Robson estimator, we estimated Z to be 0.47 ± 0.11 and A to be 0.37 .

Smallmouth Bass stomach contents collected from Starvation Reservoir contained a mixed diet that varied by month (Fig. 4). In June, aquatic invertebrates were the most common diet item in terms of mean proportion by weight (0.73) and frequency of occurrence (0.87). Crayfish and fish species were also identified in June diets, but at a lower mean proportion by weight (0.21 and 0.05, respectively) and frequency of occurrence (0.33, 0.09). Smallmouth Bass diets in July had a higher mean proportion by weight of crayfish (0.52) than diets in June, but aquatic invertebrates continued to have the greatest frequency of occurrence. Consumption of fish in July remained minimal as shown by both mean proportion by weight (0.06) and fre-

quency of occurrence (0.09). Diets collected in October were dominated by crayfish and fish prey; both mean proportion in the diet and frequency of occurrence were similar for crayfish (0.47 and 0.52) and fish (0.53 and 0.61) during October. Other prey items, such as terrestrial insects (Hymenoptera) and zooplankton, were minor components (<0.05) of Smallmouth Bass diets in terms of mean proportion by weight and frequency of occurrence.

We found that Smallmouth Bass diets contained several species of fish throughout our study, along with a mixed diet of various aquatic invertebrates in June and July when this prey type was most common. We identified 4 species of fish in the diets of Smallmouth Bass; however, the majority of fish prey items in diets were not identifiable to the species level (Table 4). Single occurrences

TABLE 4. Occurrence of lower-order prey items from subsamples of Smallmouth Bass stomach contents from Starvation Reservoir, Utah. Diets containing aquatic invertebrates in June and July ($n = 43$) were subsampled to identify prey to the order level during the period when aquatic invertebrates were proportionally the most common item in stomach samples. All diets containing fish were sampled across all seasons ($n = 19$), though most fish consumption ($n = 16$) occurred in October diets.

| Prey type | Occurrences | Frequency of occurrence (%) |
|-----------------------|-------------|-----------------------------|
| Fish | | |
| Unidentified fish | 19 | 100.0 |
| Yellow perch | 10 | 52.6 |
| Walleye | 1 | 5.3 |
| Kokanee | 1 | 5.3 |
| Smallmouth Bass | 1 | 5.3 |
| Aquatic invertebrates | | |
| Odonata | 23 | 53.5 |
| Diptera | 15 | 34.9 |
| Isopoda | 15 | 34.9 |
| Ephemeroptera | 8 | 18.6 |
| Other | 6 | 14.0 |
| Amphipoda | 5 | 11.6 |

of Kokanee Salmon (*Oncorhynchus nerka*), Walleye, Smallmouth Bass, and Yellow Perch (*Perca flavescens*) were identified in the diet during June and July. In October, Yellow Perch was the most frequently identified fish species in the Smallmouth Bass diets. Our subset ($n = 43$) of Smallmouth Bass diets collected in June and July containing aquatic invertebrates comprised 7 different orders (Table 4). The most frequently identified aquatic invertebrates were of the orders Odonata, Diptera, and Isopoda (>30% frequency of occurrence; Table 4).

Bioenergetics modeling suggested trends of decreasing p with age; however, overall GE was consistent among cohorts. We found p to be highest for age-2 fish (0.54; Table 1) and to decline throughout subsequent age classes to 0.25 for ages 8 and 9 (Table 1). The GE was consistent across cohorts, with a value of 0.18 occurring for all but the age-2 cohort (0.16; Table 1). Per-fish consumption estimates (weight) increase with each age class. For example, an age-2 Smallmouth Bass consumed an average of 571 g of prey over the 150-d period, whereas an age-9 fish consumed 924 g of prey during the same period (Table 1). Our bioenergetics model estimated that most prey consumption by Smallmouth Bass (by mass in grams) occurred in August during warmer water temperatures. By mass, crayfish were by far the most-consumed prey

item across the entire 150-d period, followed by other aquatic invertebrates and fish.

DISCUSSION

We found the Smallmouth Bass population in Starvation Reservoir to be in relatively healthy condition and to have acceptable size structure for a midelevation reservoir, consisting of good proportions of quality- and preferred-length fish that quickly recruit to the recreational fishery. Growth rates were typical of Smallmouth Bass populations at similar latitudes and were likely governed by water temperatures that remain below the thermal optimum for growth throughout the year (Mullner and Hubert 1993, Beamesderfer and North 1995, Whitley et al. 2002). We found that relative growth declined with age, and we speculate that additional factors may reduce growth in older age classes. Mortality rates were comparable to other populations that do not experience substantial harvest pressure, and it is unlikely that more restrictive creel regulations or the addition of length regulations would improve the average size of Smallmouth Bass in this midelevation reservoir (Beamesderfer and North 1995, Birchell et al. 2016). Collectively, our study provides additional data on diet, growth, mortality, and overall performance that may provide useful comparison for managers of other Smallmouth Bass populations within the Intermountain West.

Growth rates of Smallmouth Bass in Starvation Reservoir are likely driven by environmental conditions such as latitude, elevation, and their cumulative effects on water temperature; however, additional factors such as forage size or differing metabolic demands among ages could affect growth under some conditions. Smallmouth Bass in our study reached quality length within the expected age range of 3.3–4.5 years that is common to midelevation reservoirs (Beamesderfer and North 1995) and those at similar latitude (e.g., Nebraska—Schall et al. 2016). Alternately, Mullner and Hubert (1993) reported much slower growth for Smallmouth Bass populations surveyed in Flaming Gorge Reservoir, UT–WY; thus, food availability or habitat may have been more limiting to Smallmouth Bass in that system relative to Starvation Reservoir. Unsurprisingly, Smallmouth Bass populations within

the southern portion of the species' range experience faster growth than we observed, supporting the idea of temperature-influenced population performance. For example, Smallmouth Bass in Alabama neared quality length by age 2 (Slipke et al. 1998); however, faster growth may also relate to increased mortality (Beamesderfer and North 1995) and a lower average size in black bass populations. Climate change may increase the average temperature of Intermountain West reservoirs, which may extend the growing season for Smallmouth Bass and change growth dynamics for populations in this range.

Growth and prey consumption rates were not uniform across age classes; however, indices of size and condition did not suggest that food availability was substantially limiting Smallmouth Bass growth in Starvation Reservoir. We found relative growth rates to be highest for age-2 Smallmouth Bass and that RGI declined with each age class. Similarly, bioenergetics estimates of p were also highest for age-2 fish and declined with each age class. Patterns of declining p that we observed are consistent with other studies (e.g., Walleye and Smallmouth Bass—Wuellner et al. 2010). With adequate prey availability, the higher metabolic demands of smaller fishes may relate to increased p and RGI in younger ages relative to older individuals (Whitledge et al. 2002, Rosenfeld et al. 2015), particularly under thermal conditions that remained below the thermal optimum of Smallmouth Bass for much of the growing season (Whitledge et al. 2002). Furthermore, the size and availability of prey items in Starvation Reservoir may be favorable to younger age classes of Smallmouth Bass. For example, aquatic invertebrates composed a substantial portion of Smallmouth Bass diet in the early growing season. Given the small and uniform sizes of these prey items, we speculate that foraging time and subsequent feeding efficiency would be reduced for larger Smallmouth Bass relative to smaller individuals. Similarly, although size limitations of prey decrease with predator size (Schake et al. 2014, Gaeta et al. 2018), Smallmouth Bass and other predatory fishes often continue targeting prey items (e.g., forage fishes) within a certain size range (Gaeta et al. 2018), which may relate to maximizing energy intake per unit of effort (Brose 2010). This strategy would also benefit younger Smallmouth Bass, whose

consumption requirements could be met with fewer prey items. Despite declining RGI and p across cohorts, both PSD and W_r indicate that the size structure and condition of the population is within common management targets for *Micropterus* spp. (PSD 30 to 60—Gabelhouse 1984; W_r 95 to 105—Anderson 1980). Our overall estimates of p across age classes fell within the range of other models of black bass species. For example, Yako et al. (2000) found that p for Largemouth Bass ranged from 0.39 to 0.44 in a Washington Reservoir, and Moore (1988) observed that p for Smallmouth Bass in Smith Mountain Lake, Virginia, ranged from 0.26 to 0.30.

Seasonal diet changes during our study suggest that Smallmouth Bass adapt to forage availability and are able to use a wide variety of prey resources throughout the growing season. These findings are consistent with others who have studied Smallmouth Bass diets in both lotic (e.g., Dauwalter and Fisher 2008) and lentic (e.g., Wuellner et al. 2010) systems. Consumption of aquatic invertebrates was highest during the spring and declined throughout the summer to almost no consumption in the fall. Previous diet work (1998–1999) for Smallmouth Bass in Starvation Reservoir also suggests little to no aquatic insect consumption after summer months (Luecke et al. 2001). Shifts away from aquatic invertebrate prey may reflect a switch to more energy-dense diet items such as young-of-year fishes, which would have grown and become available to Smallmouth Bass later in the year. The inclusion of fish (mainly Yellow Perch) in fall diets likely coincides with age-0 forage fishes reaching targetable size and may provide an opportunity to target high-energy prey for a specific portion of the year. Similar to our study, Wuellner et al. (2010) observed that Smallmouth Bass in Lake Sharpe, South Dakota, shifted from a mixed diet of invertebrates to primarily fish later in the growing season, and they associated this trend with age-0 Gizzard Shad *Dorosoma cepedianum* becoming available. Seasonal increases in the consumption of fish by Smallmouth Bass in Starvation Reservoir may also relate to declining water levels, which could leave age-0 fishes more vulnerable to predation by piscivores as vegetated littoral zones dry and young fish are forced into deeper habitat (Zohary and Ostrovsky 2011). Specific to Starvation Reservoir, the mixed use

of both crayfish and fish in October (as opposed to solely crayfish 20 years ago—Luecke et al. 2001) may be a result of increased forage fish availability since the previous evaluation. The illegal introduction of Yellow Perch, along with UDWR introductions of Black Crappie *Pomoxis nigromaculatus* and Kokanee Salmon from 2016 to 2020, have increased the availability and diversity of forage within Starvation Reservoir.

Annual mortality rates of Smallmouth Bass were comparable to other populations with little to no harvest across the species' range. Mortality rates of 0.2 to 0.6 are characteristic of “unexploited,” “average-production” Smallmouth Bass populations (Beamesderfer and North 1995). Harvest of Smallmouth Bass is negligible in Starvation Reservoir (Birchell et al. 2016), and we assumed natural mortality to be the primary contributor to total mortality; however, hooking mortality and handling stress from catch-and-release angling may also contribute to some Smallmouth Bass mortality in Starvation Reservoir (Kerns et al. 2012). Our annual mortality estimate of 0.37 was comparable to populations at similar latitudes (0.41 in Nebraska Reservoirs—Schall et al. 2016; 0.42 in Coeur d'Alene Lake, Idaho—Walrath et al. 2015). Annual mortality may be much higher in faster-growing, southern populations (e.g., 0.53 in Tennessee—Fiss et al. 2001) or heavily exploited populations (e.g., 0.71 in Iowa—Paragamian 1984). Consequently, mortality rates observed during our study appear sustainable.

The ability to manipulate thermal conditions or coarse-scale habitat is unlikely in midelevation, western reservoirs; thus, management of Smallmouth Bass in the Intermountain West may benefit most from monitoring and maintaining food availability in these historically underproductive reservoirs. Our study was conducted during a single year, and it is likely that prey availability fluctuates annually due to variable conditions not captured during our study (e.g., nutrient differences or extreme fluctuations in reservoir elevations). This, in turn, could affect Smallmouth Bass population dynamics in ways not observed during the single-year snapshot that we examined (e.g., variable year class strength as a result of changing water levels—Sammons and Bettoli 2000). We show that naturally reproducing populations of crayfish and Yellow Perch are important prey items for

Smallmouth Bass in the late summer and fall, yet estimates of annual recruitment can be difficult to obtain for these species. Monitoring of relative abundance may provide some insight to managers. For example, annual netting of Yellow Perch populations in Starvation Reservoir over the last 5 years indicates relatively stable numbers of young-of-year and age-1 Yellow Perch (i.e., CPUE, UDWR unpublished data) and that larger Yellow Perch (>150 mm, not vulnerable to Smallmouth Bass predation—Gaeta et al. 2018) continue to occur in the population, sustaining natural reproduction each year. Smallmouth Bass in Starvation Reservoir use a variety of prey throughout the year, so management strategies that focus on maintaining or improving prey diversity (e.g., supplemental stocking of forage fishes, protection of reservoir and upstream habitat that facilitates aquatic invertebrate production) may also benefit Smallmouth Bass populations. Lastly, management of Smallmouth Bass in the Intermountain West would benefit from understanding interactions with other introduced sport fishes in these systems (e.g., Walleye—Wuellner et al. 2010), which have the potential to use the same forage resources or directly prey on young-of-year individuals.

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